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## Reconciling diverse lacustrine and terrestrial system response to penultimate deglacial warming in southern Europe

**Graham P. Wilson<sup>1\*</sup>, Jane M. Reed<sup>2</sup>, Michael R. Frogley<sup>3</sup>, Philip D. Hughes<sup>4</sup>, and  
Polychronis C. Tzedakis<sup>5</sup>**

<sup>1</sup>*Department of Geography and International Development, University of Chester,  
Chester CH1 4BJ, UK*

<sup>2</sup>*Department of Geography, Environment and Earth Sciences, University of Hull, Hull  
HU6 7RX, UK*

<sup>3</sup>*Department of Geography, University of Sussex, Brighton BN1 9QJ, UK*

<sup>4</sup>*Department of Geography, School of Environment, Education and Development,  
University of Manchester, Manchester M13 9PL, UK*

<sup>5</sup>*Department of Geography, University College London, London WC1E 6BT, UK*

\*E-mail: [graham.wilson@chester.ac.uk](mailto:graham.wilson@chester.ac.uk).

### **ABSTRACT**

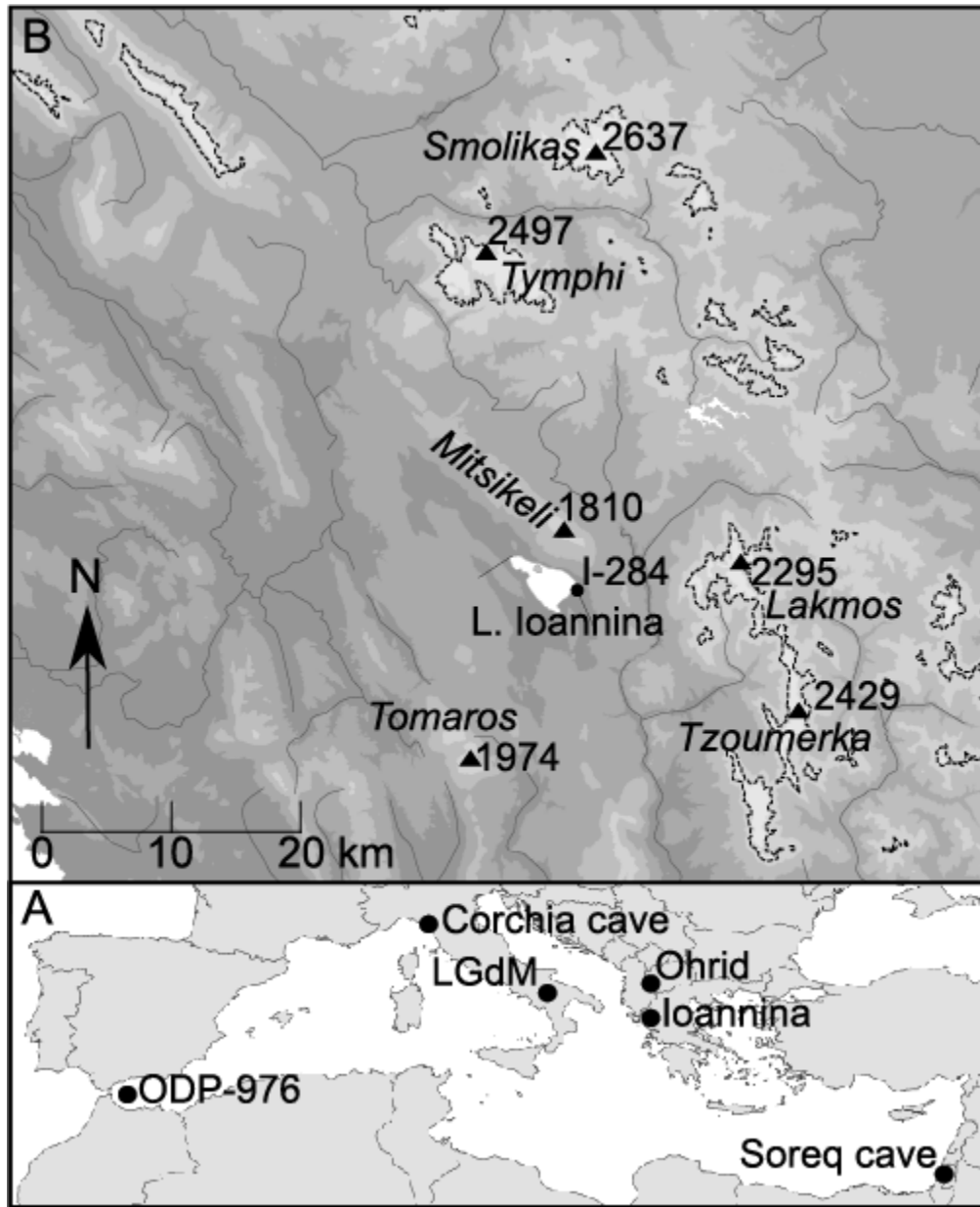
Unlike the most recent deglaciation, the regional expression of climate changes during the penultimate deglaciation remains understudied, even though it led into a period of excess warmth with estimates of global average temperature 1–2 °C, and sea

level ~6 m, above preindustrial values. We present the first complete high-resolution southern European diatom record capturing the penultimate glacial-interglacial transition, from Lake Ioannina (northwest Greece). It forms part of a suite of proxies selected to assess the character and phase relationships of terrestrial and aquatic ecosystem response to rapid climate warming, and to resolve apparent conflicts in proxy evidence for regional paleohydrology. The diatom data suggest a complex penultimate deglaciation driven primarily by multiple oscillations in lake level, and provide firm evidence for the regional influence of abrupt changes in North Atlantic conditions. There is diachroneity in lake and terrestrial ecosystem response to warming at the onset of the last interglacial, with an abrupt increase in lake level occurring ~2.7 k.y. prior to sustained forest expansion with peak precipitation. We identify the potentially important role of direct input of snow melt and glacial meltwater transfer to the subterranean karst system in response to warming, which would cause rising regional groundwater levels. This explanation, and the greater sensitivity of diatoms to subtle changes in temperature, reconciles the divergent lacustrine and terrestrial proxy evidence and highlights the sensitivity of lakes situated in mountainous karstic environments to past climate warming.

## INTRODUCTION

During the penultimate deglaciation [ca. 136–129 ka, the Marine Isotope Stage 6 (MIS 6) to MIS 5 transition, Termination II] global climate shifted from one of the most extreme glaciations to one of the warmest interglacials. Recent high-resolution marine sediment records from the Iberian margin reveal a complex multiple-step climate transition in response to deglacial meltwater pulses into the North Atlantic associated

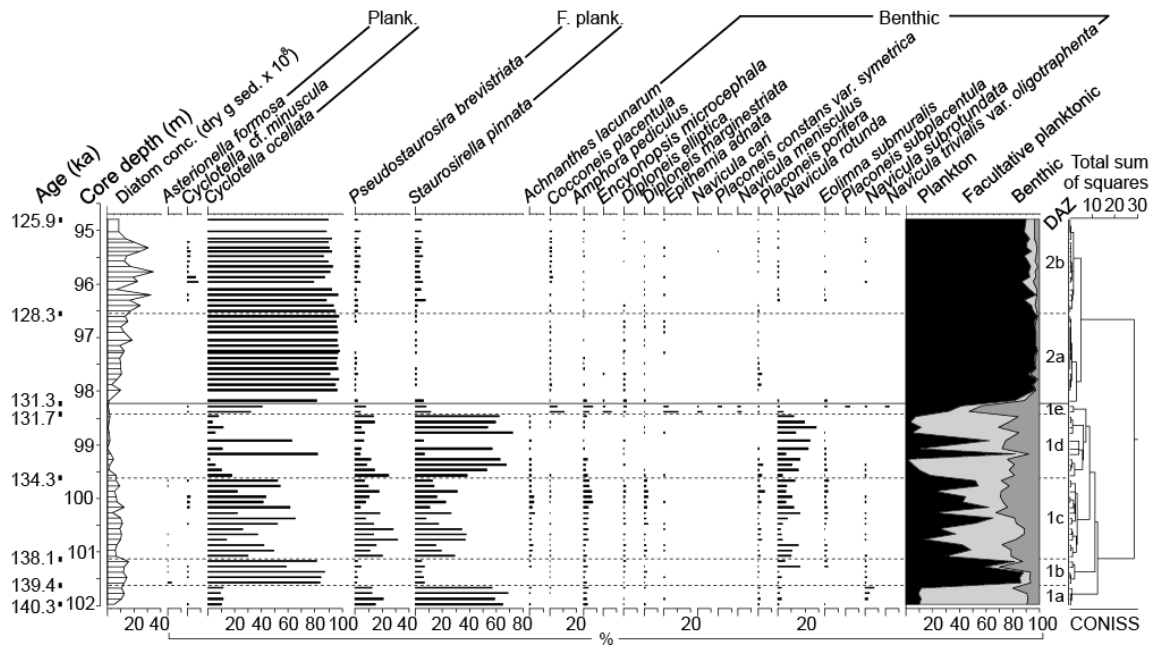
with Heinrich Stadial 11 (HS11; ca. 136–130 ka; Martrat et al., 2014; Marino et al., 2015), a pattern also seen in regional speleothem  $\delta^{18}\text{O}$  records (Drysdales et al., 2009; Grant et al., 2012). Episodes of low sea-surface temperatures (SSTs) and aridity at this time may have been caused by the expansion of North Atlantic cold water masses into lower latitudes (Martrat et al., 2014). Few data from this period are available from continental lake and peat bog archives. In Lago Grande di Monticchio, southern Italy, expansion of forests started at 130.6 ka; a short-lived (~250 yr) reduction in tree populations is apparent at 128.2–127.9 ka (Brauer et al., 2007). In Lake Ohrid (Albania-Macedonia), the absence of ice-rafted debris and rising calcite from ca. 130 ka indicate a transition to interstadial conditions, with onset of full interglacial conditions from ca. 127 ka (Vogel et al., 2010), during which limnological shifts in productivity predated forest expansion (Lézine et al., 2010). The Soreq Cave (Israel)  $\delta^{18}\text{O}$  speleothem data (Grant et al., 2012) suggest an overall gradual and moderate increase in regional precipitation from ca. 139.5 ka. Sedimentological data and climate simulations indicate increasing seasonality through the penultimate late glacial (Brauer et al., 2007; Kutzbach et al., 2014). In this study, we return to Lake Ioannina (Epirus, northwest Greece; see the GSA Data Repository<sup>1</sup> for site details), a reference site for paleoclimate research in southern Europe (e.g., Frogley et al., 1999; Tzedakis et al., 2002, 2003; Wilson et al., 2008; Roucoux et al., 2011) to improve understanding of paleohydrology and terrestrial and aquatic responses to abrupt climate change during the penultimate deglaciation.



**Figure 1.** A: Location of Ioannina (northwest Greece) and sites mentioned in the text. LGdM—Lago Grande di Monticchio; ODP-976—Ocean Drilling Program Site 976. B: Sediment core site I-284 (39°45'N, 20°51'E) in relation to the present lake (470 m asl, above sea level) and surrounding topography. Areas of land >1850 m asl (stippled line) correspond to the estimated equilibrium line altitude of glaciers in this area during the penultimate glacial. Snow cover would have been permanent in the stippled areas. Glaciers would have been larger than these stippled areas but with variable hypsometries depending on local topoclimatic factors. Adapted from Wilson et al. (2013).

## CORE I-284 DIATOM RECORD

The penultimate late glacial and last interglacial sections of sediment core I-284 (Fig. 1) from the Ioannina basin have previously been the focus of multiproxy analysis (pollen, ostracod, calcite  $\delta^{18}\text{O}$ , and  $\delta^{13}\text{C}$ ; Frogley et al., 1999; Tzedakis et al., 2003). The I-284 time scale used here is constructed by aligning the percentage of temperate tree pollen to Corchia speleothem  $\delta^{18}\text{O}$  (Drysdale et al., 2009), on the premise that the amount of precipitation in southern Europe exerts a dominant control over both the composition of vegetation and the  $\delta^{18}\text{O}$  of speleothems (Tzedakis et al., 2002; Drysdale et al., 2009; see the Data Repository). Between 101.97 m and 94.80 m (ca. 140.3 and 125.9 ka), 70 samples for diatom analysis were taken at 10 cm intervals (~200 yr resolution) or greater, sufficient to span the glacial-interglacial transition as determined from changes in arboreal pollen frequency and concentration (Tzedakis et al., 2003). Sample preparation for diatom analysis followed standard techniques (Battarbee, 1986; see the Data Repository).



**Figure 2.** Summary diatom diagram of taxa present with relative frequencies of  $\geq 2\%$ . Diatom assemblage zones (DAZ), as determined by CONISS (constrained incremental sum of square cluster analysis), and DAZ boundary ages are also shown. Plank.—plankton; F.—facultative; conc.—concentration; sed.—sediment.

Two major biostratigraphic zones can be defined: diatom assemblage zone (DAZ) 1 (101.97–98.23 m, ca. 140.3–131.3 ka) and DAZ 2 (98.23–94.80 m, ca. 131.3–125.9 ka) (Fig. 2). Diatom concentrations are generally low during DAZ 1, which contains relatively high frequencies of benthic (particularly *Navicula rotunda* Hustedt) and facultative planktonic species (small Fragilariaceae: *Staurosirella pinnata* [Ehrenberg] Williams and Round, and *Pseudostaurosira brevistriata* [Grunow] Williams and Round), but with distinct peaks (to  $>80\%$  abundance) in planktonic taxa, dominated by classic forms (with three ocelli) of *Cyclotella ocellata* Pantocsek, and accompanied by large, nonclassic forms with complex central area structure. Five subzones (DAZ 1a–DAZ 1e) can be defined based on the interchanging dominance of these taxa. DAZ 1b

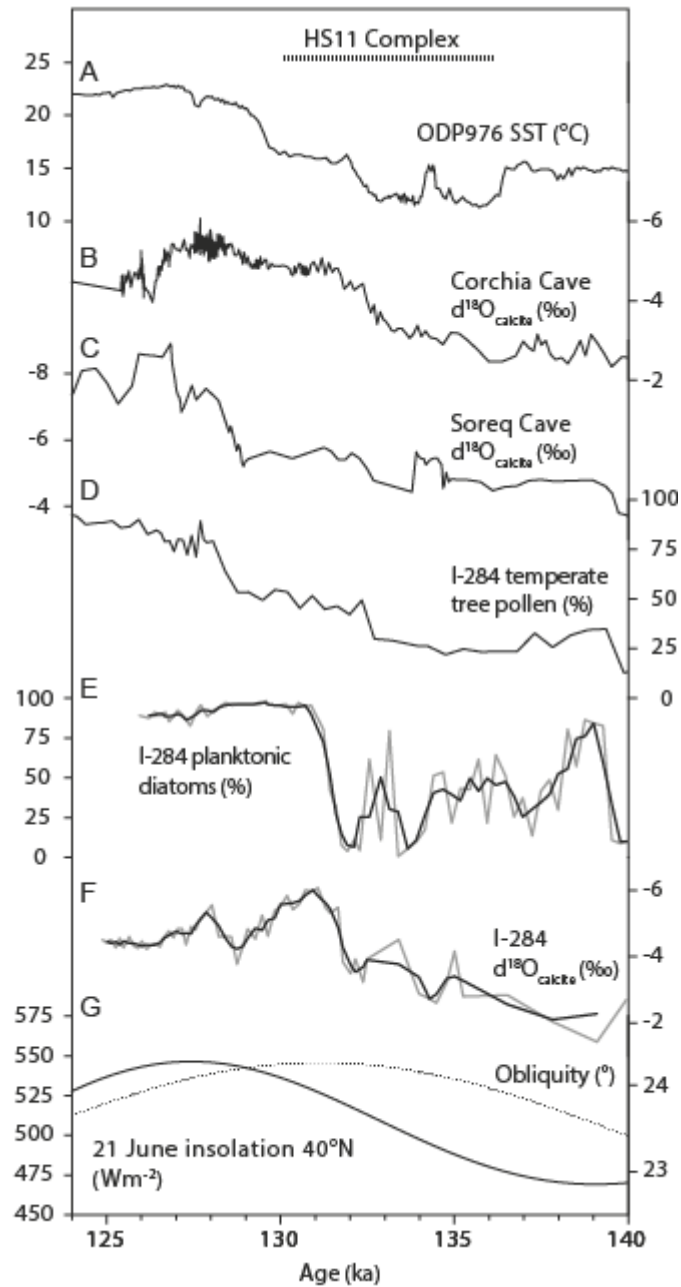
(101.62–101.12 m, ca. 139.4–138.1 ka) is notable in the consistent dominance of *C. ocellata*. A marked increase in relative abundance of *C. ocellata* occurs at the DAZ 1-DAZ 2 boundary ca. 131.3 ka at the expense of littoral taxa. Diatom concentrations in DAZ 2 are typically higher than in DAZ 1. *Cyclotella ocellata* is dominant throughout. The transition from DAZ 2a to DAZ 2b is marked by a slight increase in facultative planktonic and benthic taxa (e.g. *Cocconeis placentula* Ehrenberg, and *N. rotunda*). From previous research on the glacial diatom flora of Ioannina (e.g., Wilson et al., 2008, 2013) and other Mediterranean, relatively shallow, aquifer-fed, alkaline lakes, including Lake Dojran (Macedonia-Greece; Zhang et al., 2014) and Lake Prespa (Macedonia-Greece; Cvetkoska et al., 2014a), the small Fragilariaceae are indicative of shallow lake conditions with extended seasonal ice cover in a cold, arid glacial climate. *C. ocellata* has broad ecological preferences (in part because it is likely to represent a species complex), but in these systems, appears to indicate oligotrophic-mesotrophic conditions, particularly when accompanied by large, nonclassic forms (Cvetkoska et al., 2014a). The large Ioannina morphotypes await taxonomic description, but show affinities with recently described Mediterranean taxa separated from the *C. ocellata* complex, comprising *C. prespanensis* Cvetkoska, Hamilton, Ognjanova-Rumenova and Levkov, *C. paraocellata* Cvetkoska (Cvetkoska et al., 2014b), and *C. paleo-ocellata* Vossel and Van de Vijver (Vossel et al., 2015).

## **PENULTIMATE DEGLACIATION**

The high frequency of benthic and facultative planktonic taxa between ca. 140.3 and 131.3 ka (DAZ 1) suggests that the water depth at the core site was relatively

shallow, in a cold, arid climate. However, *C. ocellata* dominance suggests sustained higher lake levels between 139.4 and 138.1 ka (DAZ 1b). This interval coincides with a marked initial expansion in arboreal pollen from ~17% to 37% (Fig. 3), indicating an initial phase of forest expansion coeval with an inferred increase in regional precipitation (Grant et al., 2012) marking the start of the late glacial. During a period of reduced tree populations at Ioannina (ca. 137–132.5 ka), the high abundance of small Fragilariaceae and slight increase in benthic taxa suggest a return to shallow lake conditions with greater seasonal ice cover in a cold, arid climate. This is coeval with an interval of minimum SSTs in the Alboran Sea and Portuguese margin ca. 136–132 ka (Martrat et al., 2014; Fig. 3). Therefore, there is strong evidence for both terrestrial and aquatic ecosystem response at Ioannina to cooler and drier conditions associated with changes in the North Atlantic during HS11. Warming events may have punctuated stadials associated with Heinrich events, including HS11 (Martrat et al., 2014). The diatom record at Ioannina also shows short-lived peaks in *C. ocellata* at the expense of small Fragilariaceae. This may suggest short-lived episodes of higher lake levels (Wilson et al., 2008; Jones et al., 2013; Cvetkoska et al., 2014a), possibly accompanied by a longer open-water season with earlier spring ice melt (cf. Wilson et al., 2013). Lower resolution  $\delta^{18}\text{O}$  data in this section of the core prevents a robust and detailed comparison with the diatom record, but the tendency is for plankton peaks to be matched with lower  $\delta^{18}\text{O}$  values indicative of increased lake levels. Reduced forest populations and the increase in steppe elements during this interval (ca. 137–133 ka) indicate that these episodes were probably not related to increases in regional precipitation. Instead, the source of hydrological input may be from late winter pulses of groundwater flow from meltwater flooding.





**Figure 3.** Comparison of sediment core I-284 paleoecological and isotopic records with regional data sets. HS11—Heinrich Stadial 11. A: Ocean Drilling Program (ODP) Site 976 alkenone-derived sea-surface temperature (SST), western Alboran Sea (Martrat et al., 2014). B: Corchia cave (Italy) speleothem  $\delta^{18}\text{O}$  (inverted axis) (Drysdale et al., 2009). C: Soreq (Israel) speleothem  $\delta^{18}\text{O}$  (inverted axis) (Grant et al., 2012). D: Temperate tree pollen (minus *Pinus* and *Juniperus*) at Ioannina (core I-284; Tzedakis et al., 2002, 2003). E: Ioannina (core I-284) planktonic diatom frequency. F: Ioannina (core I-284)  $\delta^{18}\text{O}_{\text{calcite}}$  (inverted

axis) (Frogley et al., 1999). Black lines in E and F show the 3-point running mean, gray lines show actual data. G: 21 June insolation at 40°N and obliquity (Berger, 1978). All data are plotted on their own time scales.

The rapid transition to prolonged dominance of *C. ocellata* at the DAZ 1-DAZ 2 boundary (ca. 131.3 ka) indicates water column stability in a sustained phase of high lake level (Cvetkoska et al., 2014a). A concomitant rapid decrease in  $\delta^{18}\text{O}$  values from ca. 131.7 ka provides independent evidence of rapid lake-level rise (Fig. 3). Only a moderate increase in regional precipitation (Grant et al., 2012) and an associated intermediate expansion in tree populations at Ioannina are apparent from 132.5 ka (Fig. 3). A sharp rise in Alboran SSTs from ca. 129.5 ka (Martrat et al., 2014) is closely followed by a contemporaneous marked increase in regional precipitation (Drysdales et al., 2009; Grant et al., 2012) and in southern European tree populations between 129 ka and 128 ka (Tzedakis et al., 2003; Brauer et al., 2007). This marked increase in regional precipitation occurs 2.7 k.y. after the rapid rise in Ioannina lake level. Therefore, there is an apparent inconsistency in the timing of the main increase in regional precipitation as inferred from Ioannina lake-level changes and from changes in vegetation during the penultimate late glacial.

To explain this divergence, we suggest that regional groundwater levels may have risen during the penultimate late glacial as a result of the transfer of Pindus mountain glacial meltwater to the subterranean karst system, which is well developed in this area (see the Data Repository), and by input from snow melt. During the penultimate glacial, large glaciers existed on Mount Tymphi, with frontal moraines on the southern slopes situated ~25–30 km north of Ioannina (Hughes et al., 2007). A total of 14 glaciers

covered an area of 21.3 km<sup>2</sup> on Mount Tymphi, with an average equilibrium line altitude of 1862 m asl (above sea level). Similar-sized glaciers would have also formed on Mount Lakmos/Peristeri (2295 m asl), <15 km east of Ioannina, and the neighboring Tzoumerka/Athamanika Massif (2429 m asl), both of which have a glacial geomorphology similar to that of Mount Tymphi. These massifs currently record the largest precipitation totals in Greece (Fotiadi et al., 1999), and, if precipitation distribution was similar in glacial stages, then this would have been favorable for the formation of some of the largest glaciers in Greece (Fig. 1). Permanent snow fields and possibly small niche glaciers are likely to have formed on the slopes of Mount Mitsikeli (1813 m asl), the most immediate mountain catchment to Lake Ioannina. An increase in lake sediment calcite content at Lakes Ioannina and Ohrid ca. 132 ka and ca. 130 ka, respectively (Frogley, 1997; Vogel et al., 2010), and an absence of ice-rafted debris in Ohrid from ca. 130 ka (Vogel et al., 2010) indicate regional climate warming, even though freshwater flux from ice sheets may have prolonged stadial conditions in the North Atlantic. A warming climate would increase snow and ice melt rates, resulting in glaciers retreating upvalley to higher elevations, particularly if associated with increased rainfall in this humid, refugial location (Tzedakis et al., 2002). Moraine calcite cements in the mountains of both Greece and Montenegro yield corrected U-series ages dating to the last interglacial, with the earliest and most precise ages yielding a tight range (n = 5) ca. 124.6–120.2 ka (maximum error at 2σ = 5.3%) (Hughes et al., 2007, 2010, 2011). This indicates that glaciers had retreated from their most extensive MIS 6 positions by this time and that the moraines had stabilized, with their surfaces developing respiring soils, promoting the formation of secondary carbonate cements. Glacier retreat in

response to rising temperatures during the penultimate late glacial would have led to karst reactivation and the release of significant amounts of meltwater discharge to surface waters and groundwater aquifers through the karst (cf. Adamson et al., 2014). The combination of accelerated subterranean and surface water input would account for the rapid rise in lake level at Ioannina ca. 131.7 ka. In this context, lacustrine and terrestrial proxies would not be responding to a common driving mechanism. If local conditions are playing an important role in modulating lake response to climate change at Ioannina, then no apparent conflict between the lacustrine and terrestrial proxy evidence remains.

According to the pollen record, the onset of the last interglacial at Ioannina is placed ca. 128.6 ka, in line with a rapid shift in climate conditions from a number of Mediterranean records for that time (Fig. 3). From ca. 128.3 ka (DAZ 2b), the diatoms suggest minor lake-level reduction. This is in agreement with overall higher  $\delta^{18}\text{O}$  values, perhaps reflecting increased summer aridity and evaporation and a reduction or cessation in snowmelt and glacial meltwater input, coeval with an expansion in sclerophyllous woodland (Tzedakis et al., 2003). Taken together, these indicators of summer conditions are in line with the general framework of accentuated seasonality of precipitation during the early interglacial (Milner et al., 2012).

## CONCLUSIONS

Diatom evidence for multiple oscillations in lake level, and possibly thermal regime, at Lake Ioannina (northwest Greece) provide firm evidence for the regional influence of abrupt changes in the North Atlantic during the HS11 stadial, and add to growing regional evidence for a complex penultimate deglacial. Snowmelt and glacial

meltwater transfer are identified as primary driving mechanisms for an abrupt increase in lake level almost 3 k.y. prior to regional forest expansion and associated peak precipitation at the onset of the last interglacial. This finding has wider implications in demonstrating that, under certain boundary conditions, lakes in mountainous karstic environments are highly sensitive to past climate warming because of the role of local glaciers in controlling regional groundwater levels.

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<sup>1</sup>GSA Data Repository item 2015xxx, site details, methods, chronology, diatom data, are  
available online at [www.geosociety.org/pubs/ft2015.htm](http://www.geosociety.org/pubs/ft2015.htm), or on request from  
editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO  
80301, USA.

## DATA RESPOSITORY

## STUDY SITE DETAILS

The Ioannina basin is a polje thought to have formed during the Late Pliocene to Early Pleistocene (Clews 1989). The basin is c. 30 km long and up to 15 km wide, with a bedrock of Mesozoic and early Cenozoic limestones overlain by Pliocene and Quaternary lake sediment deposits. Artificial drainage has resulted in a reduced lake area of 22 km<sup>2</sup>, with a mean water depth of 4–5 m (but up to 11 m in places). Mt. Mitsikeli (1,810 m above sea level, a.s.l.) forms the NW edge of the basin. To the SE, the topography slopes towards Mt. Tomaros (1,974 m a.s.l.), and the Ionian Sea is located 40 km beyond. Lake Ioannina forms the base level of a karst aquifer that underlies Mt. Mitsikeli.  $\delta^{18}\text{O}$  and  $\delta\text{D}$  analysis of modern lake water demonstrates evaporative enrichment (Wilson et al., 2013), although the low mean water conductivity (0.3 mS cm<sup>-1</sup>) is within the range of modern eutrophic waters and suggests that mechanisms currently exist which maintain a freshwater state (Wilson et al., 2008). The modern lake lacks a surface outflow; the freshwater state may result from subterranean outflows via periodically unblocked sinkholes (Higgs et al., 1967) and/or natural outflows through small streams sinking beneath the limestone (Waltham, 1970). Lake Ioannina remained fresh throughout the Late Pleistocene to mid-Holocene despite fluctuations in level (Wilson et al., 2008; Jones et al., 2013), confirming the long-term hydrological influence of groundwater in this karstic system, and the potential for considerable groundwater throughflow.

## **METHODOLOGY**

Core I-284 (39°45'N, 20°51'E) from the Ioannina basin was recovered in 1989 by the Greek Institute of Geology and Mineral Exploration. Preparation of samples for diatom analysis followed standard techniques, using hot H<sub>2</sub>O<sub>2</sub> and HCl, with Naphrax™ as a slide mountant (Battarbee, 1986). During the preparation of oven-dried, weighed sediment samples of c. 0.1 g for diatom analysis, known quantities of plastic microspheres were added at the final stage for calculation of absolute diatom concentrations (Battarbee and Kneen, 1982), variations in which may reveal changes in diatom productivity, sedimentation rates and/or diatom preservation (Wolfe, 1997). Other details are given in the main text. Diatoms were analysed at x1000 magnification, using a Zeiss Axioscop 2 *plus* binocular microscope under phase contrast. Diatom preservation was sufficient to allow  $\geq 500$  valves to be counted per level. Identification is based on Krammer and Lange-Bertalot (1986, 1988, 1991a, b) and Levkov et al. (2007), adopting current diatom nomenclature. Stratigraphic zone boundaries were defined using CONISS (Grimm, 1987) on square-root transformed data. Diatom data from core I-284 are presented in Table S1.

## **DEVELOPMENT OF CHRONOLOGICAL FRAMEWORK**

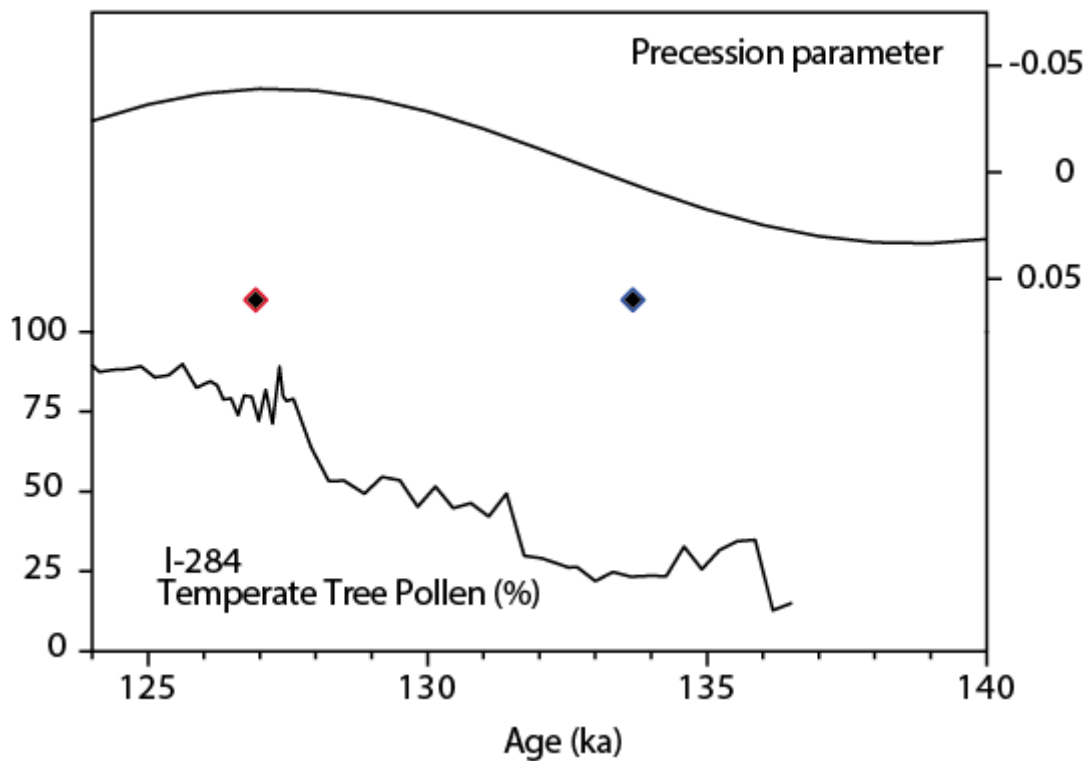
A persistent handicap in the study of the Last Interglacial has been the lack of precise absolute timescales from lake sediment sequences. While palaeomagnetic evidence and U-series dates on sediments have been used to provide a broad chronostratigraphical context, i.e. assignment to the right chronostratigraphic stage (e.g.

Frogley et al., 1999), they are not sufficiently precise to allow a precise timescale and a detailed assessment of phase relationships with other reference climate records.

An ideal situation would be annually laminated sequences anchored by tephrochronological markers, but given that these are a rare occurrence (e.g. Brauer et al., 2007), alternative approaches to developing terrestrial chronologies for the majority of sequences need to be explored: (1) direct pollen-orbital tuning, using recurrent patterns of vegetation change associated with climate conditions linked to specific orbital configurations (Magri and Tzedakis, 2000; Tzedakis et al., 2002, 2003); (2) alignment to speleothem records, on the basis that changes in the amount of precipitation would affect synchronously vegetation composition and speleothem  $\delta^{18}\text{O}$  signatures; (3) alignment to marine chronologies by correlating to pollen records from marine cores. The underlying hypothesis in alignment approaches (2) and (3) is that in records lying within the same climate province, isotopic and vegetation changes would be sufficiently time-parallel to permit the linking of records.

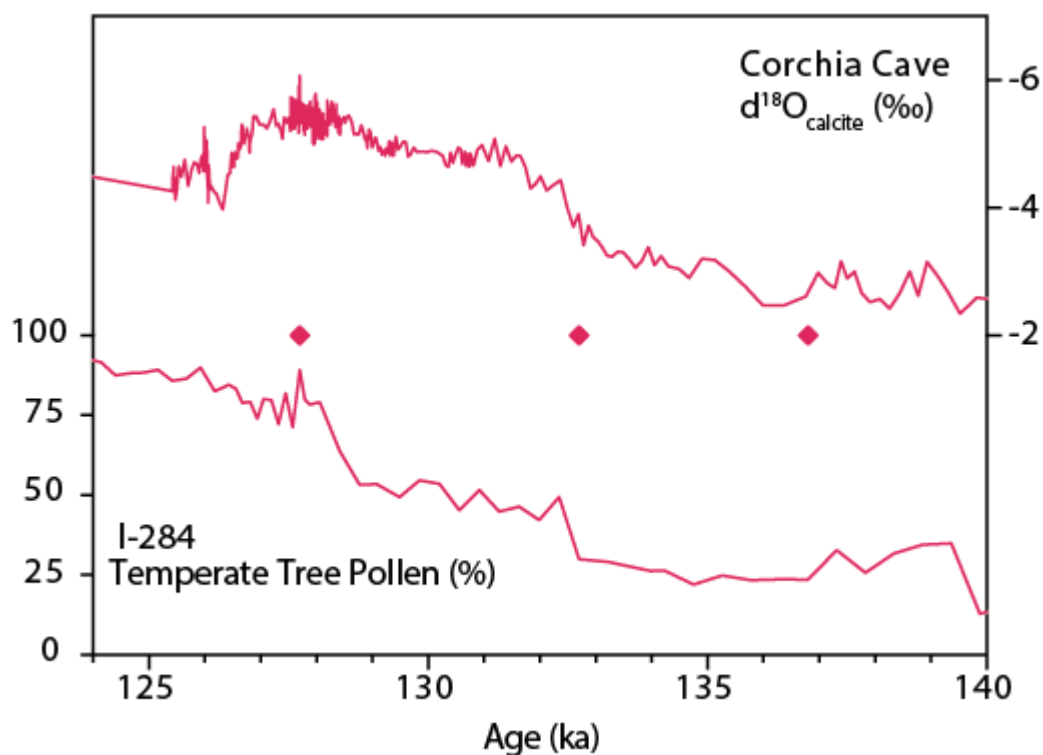
Recently Govin et al. (in review) applied these different approaches to the Last Interglacial section of the Ioannina sequence, NW Greece, to compare their relative offsets and uncertainties (Fig. S1–S4). More specifically, in addition to the original chronology based on pollen-orbital tuning (Tzedakis et al., 2002, 2003), the Ioannina 284 record was aligned to the speleothem  $\delta^{18}\text{O}$  record from Corchia Cave, Italy (Drysdalet al., 2009), and the pollen record from marine sequence MD95-2042 from the Portuguese margin (Shackleton et al., 2003) on the GL<sub>T</sub>\_syn chronology of Barker et al. (2011). Combined uncertainties arising from resolution and alignment errors and absolute dating errors in the reference sequence are 2.0–2.3 kyr for orbital tuning, 1.0–1.7 kyr for

alignment to Corchia and 1.5–1.7 kyr for alignment to MD95-2042 on the  $GL_{T\_syn}$  timescale. This sensitivity analysis reveals convergence on the timing of the interglacial onset (~128.1–128.6 ka). By comparison, there is a wider spread of ages for the onset of the lateglacial stadial (134.3–136.8 ka) due to alignment uncertainties in the penultimate glacial section of the sequences. Nonetheless, all ages fall within the chronological uncertainties of the different approaches. Here, we have used the alignment to Corchia Cave, as it represents the best-dated record in relative geographical proximity.



**Figure. S1.** Direct pollen-orbital tuning, using patterns of vegetation change associated with climate conditions linked to specific orbital configurations: the late glacial tree population minimum is aligned with the timing of perihelion passage in March (blue diamond) and the maximum in mediterranean sclerophylls with the timing of perihelion passage in June (red diamond) (Magri and Tzedakis, 2000; Tzedakis et al., 2002, 2003). Precession parameter(reversed axis) from Berger (1978).

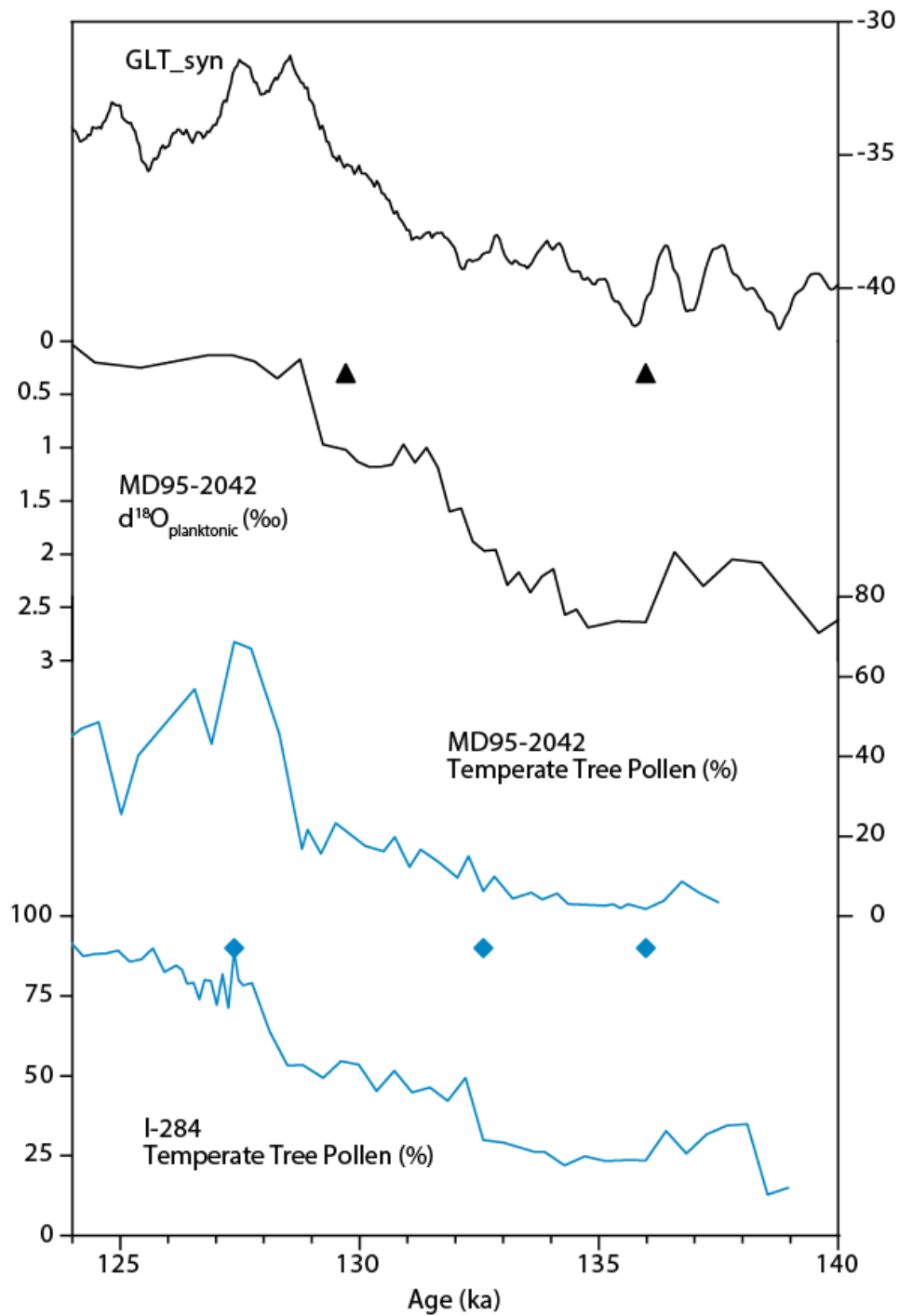
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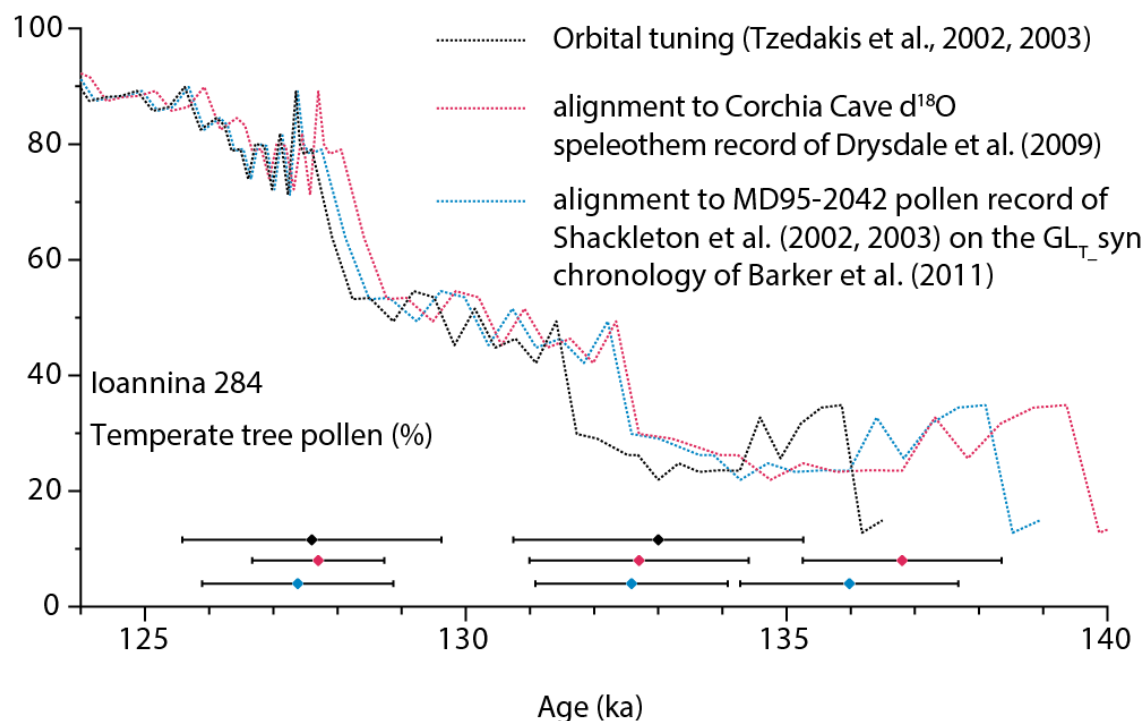
436 **Figure S2.** Alignment of the I-284 pollen record to Corchia Cave calcite  $\delta^{18}\text{O}$  record (Drysedale et al.,  
437 2009). Diamonds denote the position of alignment points.

438



**Figure S3.** Alignment of the I-284 pollen record to the pollen record of marine sequence MD95-2042 on the Portuguese margin (Shackleton et al., 2002, 2003). The timescale of MD95-2042 is based on alignment of its planktonic  $\delta^{18}\text{O}$  record on the GLT\_syn chronology of Barker et al. (2011). Diamonds and triangles denote the position of alignment points.





**Figure S4.** Comparison of different alignment methods to develop chronologies for the I-284 record.

Diamonds at the base of the diagram denote the position of control points for each scheme with the combined 1s chronological uncertainties arising from resolution, alignment errors and absolute dating errors (modified from Govin et al., in review).

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536

537 Table S1. Relative abundance of dominant ( $\geq 2\%$ ) diatom species listed by sample depth in core I-284. Diatom concentration data and  
538 the total number of valves counted are also shown.

I-284 core depth (m)	Diatom concentration (dry g sed. x10 <sup>8</sup> )	<i>Asterionella formosa</i>	<i>Cyclotella</i> cf. <i>minuscule</i>	<i>Cyclotella ocellata</i>	<i>Pseudostaurosira brevistriata</i>	<i>Staurosirella pinnata</i>	<i>Achnanthes lacunarum</i>	<i>Cocconeis placentula</i>	<i>Amphora pediculus</i>	<i>Encyonopsis microcephala</i>	<i>Diploneis elliptica</i>	<i>Diploneis marginestriata</i>	<i>Epithemia adnata</i>	<i>Navicula cari</i>	<i>Navicula constans</i> var. <i>symmetrica</i>	<i>Navicula menisculus</i>	<i>Placoneis porifera</i>	<i>Navicula rotunda</i>	<i>Eolimna submuralis</i>	<i>Placoneis subplacentula</i>	<i>Navicula subrotundata</i>	<i>Navicula trivialis</i> var. <i>oligotraphenta</i>	Plankton	Facultative planktonic	Benthic	Total valves counted
94.80	8.7	0	0	90	2	4	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	90	6	4	529	
95.02	8.8	0	0	88	4	4	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	88	7	4	537	
95.15	13.9	0	0	92	2	2	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	92	4	4	527	
95.22	21.0	0	1	90	1	5	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	91	6	3	520	
95.32	30.5	0	0	90	3	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	91	7	2	524	
95.39	24.8	0	2	92	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	94	4	2	520	
95.48	14.8	0	2	86	3	5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	88	9	3	520	
95.58	12.5	0	1	90	3	3	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	91	5	4	512	
95.67	17.4	0	0	93	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93	5	1	500	
95.77	34.7	0	1	91	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	92	5	4	510	
95.87	19.2	0	6	87	1	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	93	5	3	528	
95.96	22.6	0	8	79	4	5	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	87	9	5	502	
96.10	6.9	0	0	93	1	4	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	93	5	2	503	
96.20	32.4	0	0	97	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	97	1	2	538	
96.30	16.5	0	0	88	2	7	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	89	9	3	505	

96.40	24.4	0	0	93	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	93	3	4	538
96.50	17.6	0	0	95	2	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	95	3	2	539	
96.60	13.2	0	0	98	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	98	1	2	516	
96.70	15.2	0	0	96	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	96	1	3	515	
96.80	9.9	0	0	97	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	97	0	3	501	
96.90	13.0	0	0	97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	97	0	3	516	
97.05	18.9	0	0	97	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	97	0	3	506	
97.15	9.4	0	0	97	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	97	0	3	518	
97.25	12.7	0	0	99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	99	0	1	517	
97.28	12.0	0	0	97	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	97	1	2	501	
97.38	9.7	0	0	96	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	96	1	3	506	
97.48	10.0	0	0	96	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	96	1	3	494	
97.58	10.1	0	0	97	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	97	0	3	509	
97.68	10.7	0	0	91	2	1	0	0	0	0	1	0	0	0	0	3	0	0	0	0	0	91	2	7	528	
97.78	7.4	0	0	98	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	98	1	2	532	
97.88	3.6	0	0	95	0	0	0	1	1	0	1	0	0	0	0	2	0	0	0	0	0	95	1	5	500	
97.98	9.9	0	0	96	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	96	1	3	507	
98.18	1.3	0	0	81	2	6	0	0	2	0	2	1	0	0	0	0	0	1	0	0	0	81	8	11	508	
98.28	0.8	0	1	41	7	8	0	5	7	1	2	0	3	1	3	2	1	1	1	4	1	3	42	15	43	508
98.38	1.2	0	0	32	4	11	0	10	4	6	2	1	11	4	0	3	1	4	0	0	0	32	15	53	518	
98.47	2.5	0	0	8	14	62	1	0	2	0	0	0	0	0	0	0	12	0	0	0	0	8	76	16	508	
98.57	1.3	0	0	4	14	59	0	0	1	0	0	0	0	0	0	0	20	0	0	0	0	4	74	23	510	
98.67	1.1	0	0	11	4	54	0	0	1	0	0	0	0	0	0	0	28	0	0	0	0	11	58	31	507	
98.77	1.3	0	0	5	7	72	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	5	79	16	501	
98.92	2.4	0	0	62	6	6	1	0	0	0	0	0	0	0	0	0	23	0	0	0	0	62	12	26	525	
99.07	0.4	0	0	11	4	57	0	0	1	0	0	0	0	0	0	1	22	1	0	0	0	11	61	28	498	
99.17	2.6	0	0	82	4	6	0	0	0	0	0	0	0	0	0	0	6	1	0	0	0	82	10	8	524	
99.27	5.0	0	0	1	12	63	1	0	3	0	0	0	0	0	0	1	17	1	0	0	0	1	74	24	509	

99.37	1.9	0	0	6	8	67	1	0	1	0	1	0	0	0	0	0	3	10	0	0	0	0	6	76	19	503
99.47	1.4	0	0	10	14	53	1	0	2	0	0	0	0	0	0	0	1	15	1	0	0	0	10	67	23	508
99.57	7.0	0	0	18	25	38	1	0	3	0	0	1	0	0	0	0	3	3	0	0	0	0	18	63	19	514
99.67	6.8	0	0	52	7	13	1	0	4	0	0	2	0	0	0	0	1	13	3	0	0	0	52	19	29	519
99.77	9.3	0	0	54	9	14	1	0	4	0	1	2	0	0	0	0	2	6	2	0	0	0	54	23	23	517
99.87	5.3	0	0	22	18	31	1	0	6	0	2	3	0	0	0	0	5	6	2	0	0	0	22	49	29	528
99.97	6.9	0	2	43	10	16	3	0	6	0	1	3	0	0	0	0	1	11	1	0	0	0	45	26	29	507
100.07	7.3	0	1	41	8	22	3	0	7	0	0	1	0	0	0	0	2	5	1	0	0	0	43	30	27	529
100.17	12.6	0	1	61	4	10	1	0	4	0	0	2	0	0	0	0	0	12	1	0	0	0	62	14	24	507
100.27	3.9	0	0	22	19	26	4	0	3	0	0	1	0	0	0	0	1	17	2	0	0	0	22	45	33	507
100.37	10.0	0	0	65	8	8	1	0	4	0	1	2	0	0	0	0	0	7	1	0	0	0	65	16	19	508
100.47	11.7	0	0	52	13	17	1	0	2	0	1	3	1	0	0	0	1	3	1	0	0	0	52	31	17	504
100.57	9.2	0	0	26	28	34	1	0	3	0	0	0	0	0	0	0	2	2	0	0	0	0	26	63	12	517
100.67	11.0	0	0	37	13	38	1	1	2	0	1	1	0	0	0	0	1	3	0	0	0	0	37	51	12	573
100.77	10.3	0	0	14	31	37	1	0	4	0	0	0	0	0	0	0	3	3	0	0	1	0	14	68	17	502
100.87	7.3	0	0	42	16	15	2	0	2	0	1	1	0	0	0	0	0	15	1	0	0	0	42	30	28	514
100.97	6.4	0	0	49	11	19	2	0	1	0	0	2	0	0	0	0	1	10	1	0	0	0	49	30	21	522
101.07	6.9	0	0	30	20	29	1	0	2	0	1	1	0	0	0	0	2	10	0	0	1	0	30	49	21	509
101.17	15.8	0	0	81	2	5	1	0	2	0	1	0	0	0	0	0	0	5	1	0	0	0	81	6	13	505
101.27	12.5	0	1	58	4	7	1	0	3	0	1	0	0	0	0	0	0	16	2	0	1	0	59	11	30	526
101.37	11.9	0	0	87	1	5	0	0	1	0	1	2	0	0	0	0	1	0	0	0	0	0	88	6	7	500
101.47	14.4	0	1	85	1	6	0	0	1	0	0	1	0	0	0	0	0	2	0	0	1	0	85	7	7	513
101.57	12.7	3	0	83	1	6	0	0	2	0	0	0	0	0	0	0	0	1	0	0	1	0	86	7	7	535
101.67	10.7	0	0	11	12	57	1	0	3	0	0	1	0	0	0	0	1	2	0	0	6	0	11	69	20	515
101.77	13.1	0	0	9	12	69	0	0	2	0	0	0	0	0	0	0	1	1	0	0	3	0	9	81	10	534
101.87	10.7	0	0	11	21	59	0	0	2	0	0	0	0	0	0	0	1	2	0	0	2	0	11	80	9	510
101.97	5.5	0	0	10	15	65	0	0	3	0	0	1	0	0	0	0	1	0	0	0	0	0	10	80	10	508